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Phenological patterns and life history tactics of Helicoidea (Gastropoda, Pulmonata) snails from Northern Greece

Patrones fenológicos y estrategias de vida en Helicoidea (Gastropoda, Pulmonata) del Norte de Grecia

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ABSTRACT

The present study mainly concerns with the differences in the biological cycles and strategies adopted by different Helicoidea snail species. In Northern Greece the climatic conditions are not very uniform. Some snails breed during the same period as in Northern Europe but most breed in autumn, as species from Southern Europe do. Breeding may take place in all seasons except in winter, and seems to be species-specific. Long-lived snails of big size differ from short-lived species of small size as to the time of their breeding period. The climatic conditions affect the time of the breeding season and their whole life cycle and phenologies. Environmental variables in Northern Greece are strongly seasonal and thus Helicoidea snails exhibit predictable oscillations in their activity patterns, which can be interpreted by the demographic response of the populations. Terrestrial snails seem to follow two different phenologic curve types: the semelparous and short-lived species populations show a more stable phenological pattern than the biennial and pluriennial ones, who mature after the first year of their lives, being more plastic trying to face the climatic differences from one year to another.

RESUMEN

El presente estudio trata de las diferencias en los ciclos biológicos y a las estrategias adoptadas por diferentes especies de Helicoidea. En el norte de Grecia, las condiciones climáticas no son muy uniformes. Algunas especies crían durante el mismo periodo en que lo hacen en el N de Europa, pero la mayoría lo hacen en otoño, como sucede en especies del S del continente. La cría puede tener lugar durante casi todas las estaciones, excepto el invierno, y el periodo parece ser específico para cada especie. Las especies longevas y de gran talla difieren de las de pequeño tamaño y vida más corta en la duración de su ciclo de cría. Las condiciones climáticas afectan al momento de la temporada de cría y a todo su ciclo vital y fenología. Las variables ambientales son fuertemente estacionales, así que aparecen oscilaciones predecibles en los patrones de actividad, que pueden ser interpretadas por la respuesta demográfica de las poblaciones. Las babosas parecen seguir dos tipos de curvas fenológicas distintas. Las especies semelpáricas y de corta vida muestran un patrón fenológico más estable que el de especies bianuales y prurianuales, que maduran tras el primer año de vida y son más flexibles a la hora de enfrentarse a las diferencias climáticas interanuales.

KEY WORDS: Biological cycle, phenology, Northern Greece, Helicoidea, *Helix*, *Eobania*, *Helicella*, *Monacha*, *Bradybaena*.

PALABRAS CLAVE: ciclo biológico, fenología, N Grecia, Helicoidea, *Helix*, *Eobania*, *Helicella*, *Monacha*, *Bradybaena*.

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INTRODUCTION

Greece has a Mediterranean climate which is differentiated mainly along a northern-southern gradient. In Northern Greece climate is transient from Mediterranean (mostly coastal areas) to temperate (inland areas). A typical characteristic of this climate type is the coincidence of high temperatures and low precipitations during summer (lasting from June to October). The wet season is divided by a cold winter which is milder in the coastal areas. Drought is a strong agent controlling population dynamics and activity of most soil invertebrates as it imposes a pause in most physiological activities. Low temperatures during winter are also important for population dynamics and activity as they impose hibernation in some of the invertebrates e. g. terrestrial gastropods. So observed discontinuities in population development during the transition from the favourable to the unfavourable seasons and vice-versa may be attributed to environmental thresholds.

Although the association between climate and life history phenomena is self evident, it can vary among terrestrial molluscs, even between populations of the same species. Phenology reflects certain aspects of the demography of a population, that is the timing of its life cycle characteristics in a given environment. The classification of phenological patterns into categories or types (WOLDA, 1988) is better by using phenological models (VAN STRAALEN, 1982; STAMOU, ASIKIDIS, ARGYROPOULOU AND SGARDELIS, 1993). Using a phenological model, complex phenograms can be classified into types considering their skewness, curtosis, phase and period.

The aim of the present study was to find out whether terrestrial gastropods adopt a general phenological pattern if they are differentiated according to their origin, or their biotopes (inland and coastal areas) or life spans. The present study is a part of an extensive research done on the distribution and ecology of Helicoidea gastropods in Northern Greece (LAZARIDOU-DIMITRIADOU, 1981, 1995; LAZARIDOU-DIMITRIADOU AND KATTOULAS, 1981, 1985, 1991; STAIKOU, LAZARIDOU-DIMITRIADOU AND FARMAKIS, 1988; HATZIIOANNOU, ELEUTHERIADIS AND LAZARIDOU-DIMITRIADOU, 1989; STAIKOU, LAZARIDOU-DIMITRIADOU AND PANA, 1990; STAIKOU AND LAZARIDOU-DIMITRIADOU, 1990, 1991).

MATERIALS AND METHODS

Data used derived from monthly quantitative samplings of Helicoidea snails from different parts of Northern Greece. The following species were studied: Family Bradybaenidae, *Bradybaena fruticum* (Müller, 1774); Family Helicidae, *Cepaea vindobonensis* (Férussac, 1821), *Eobania vermiculata* (Müller, 1774), *Helix lucorum* Linnaeus, 1758, *Helicella (Xerothracia) pappi* (Schüt, 1962), *Helix figulina* (Rossmässler, 1839), *Helix pomatia rhodopensis* Kobelt, 1906, *Theba pisana* (Müller, 1774); Family Hygromiidae, *Cernuella virgata* (Da Costa, 1778), *Monacha cartusiana* (Müller, 1774), *Xerolenta obvia* (Menke, 1828), *Xeropicta arenosa* Ziegler, 1836, *Xerotricha conspurcata* (Draparnaud, 1801). Sampling lasted two or four years depending on the species and their life span (LAZARIDOU-DIMITRIADOU, 1981, 1995; LAZARIDOU-DIMITRIADOU AND KATTOULAS, 1981, 1985, 1991; STAIKOU *ET AL.*, 1988; STAIKOU *ET AL.*, 1990; STAIKOU AND LAZARIDOU-DIMITRIADOU, 1990, 1991). Details regarding the sites and the sampling procedures are given in previous studies on these species (LAZARIDOU-DIMITRIADOU, 1981, 1995; LAZARIDOU-DIMITRIADOU AND KATTOULAS, 1985, 1991; STAIKOU *ET AL.*, 1988). Ombrothermic data for Northern Greece from 1980 to 1990 are given in Figure 1. Data were provided by Mahairas P., Professor of Climatology from the Aristotle University of Thessaloniki.

Fischer's exact test for independence in 2 x 2 contingency tables (ZAR, 1984) was used for comparisons between the different categories, e. g. snails with autumnal and vernal-estival reproductive periods, long-lived (> 3 years) and

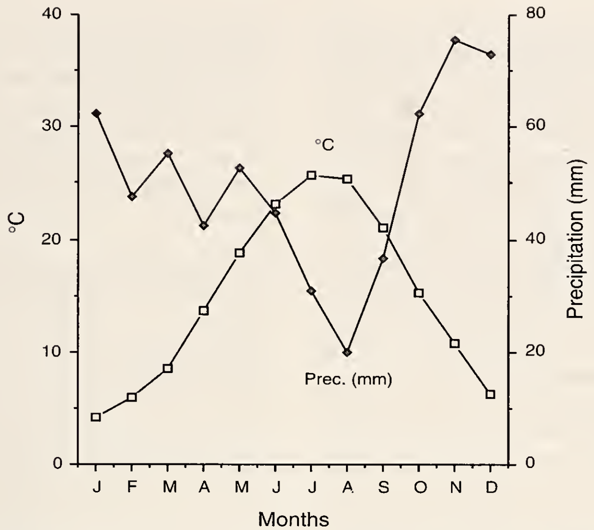

Figure 1. Ombrothermic diagram from Northern Greece. Temperature: open squares; Precipitation: solid rhombus.

Figura 1. Diagrama ombrotérmico del Norte de Grecia. Temperatura: cuadrados abiertos; Precipitación: rombos sólidos.

short-lived snail species (up to 3 years), large (largest shell diameter > 25 mm) and small sized snails.

The phenological pattern of Helicoidea species was studied by using the phenological model applied for the study of microarthropods (Stamou *et al.*, 1993). In short, in this model when asymmetries and discontinuities are displayed the scales of the time-axis were adjusted. Changing time scales results in the definition of a new variable termed ecological time (ET), which is a function of a standard clock time (Stamou *et al.*, 1993). This technique is based upon the following considerations: 1) the timing of a population in the field is determined by the sequence of demographic events and/or behavioural characteristics (i. e. migratory), and 2) the rate of the demographic events depends on the fluctuations of environmental variables.

In this model it is assumed that the phenology of any population inhabiting a seasonal environment can be described by a symmetric periodic curve:

$f(\mathrm{ET}) = \mathrm{EXP}(\alpha + b \times \mathrm{COS}(2\pi \times (\mathrm{ET} - \varphi / T))$ (1)

where the independent variable ET, termed Ecological time, is a function of standard clock time (ST), ET = f (ST). In the course of standard time, ecological time is going faster during periods of sharp changes in abundance and slower during periods of abundance stability. Thus, the proposed equation describing the length of the Ecological time unit (ΔET) as a function of Standard time ST is:

$\Delta\mathrm{ET} = f(\mathrm{ST}) = \mathrm{EXP}(\alpha_1 + b_1 \times \mathrm{COS}(2\pi \times (\mathrm{ST} - \varphi_1)/T_1))$ (2)

The model has eight parameters of which the period T and the phase φ of the phenogram, as well as period T_1 and the phase φ_1 of the function relating ET to ST, are the most important. The period T and the phase φ of the phenograms are expressed formally in ET units. For convenience they could be expressed in ST units (as T′ and φ′) by using equation (2) for the calculation of the Standard time T′ or φ′ which corresponds to T or φ units in the Ecological time-scale (see STAMOU *ET AL.*, 1993: fig. 1). For the comparison of phenograms two more parameters can be derived: a) an estimation of the sharpness (curtosis) of the phenogram $C=(R_2-R_1)/T'$, where (R_2-R_1) is the time interval around the phase φ′, during which the abundance is above overall mean, and b) an estimation of the skewness of the phenogram $S= (\varphi'-\varphi_m)/T'$ where φ_m is the time (in ST units) when the abundance of the population is at minimum. Thus, phenograms displaying a peak at $\varphi'-\varphi_m = T'/2$ (half period) is symmetric (S= 0.5), phenograms displaying a peak soon after the minimum (S< 0.5) are positively skewed, and phenograms with S> 0.5 are negatively skewed. The model was fitted on log-transformed census data. For $ET_i= f(ST_i)$ given as a time vector and for a given set of φ and T, the parameters a and b were estimated by least-square regression.

RESULTS

The model fitted to census data for snail populations sampled at monthly intervals from different areas are shown in Figure 2. The values of the most important parameters of the fitted phenological model are given in Table I.

In all but two examined cases the phenological pattern was strongly seasonal (Fig. 2), with a more or less 1 year periodicity apart from *Monacha cartusiana* which seems to display a six months periodicity at least during 1984 (Table I). Abundance of *Bradybaena fruticum* and *Eobania vermiculata* fluctuated almost randomly throughout the year.

Population densities of the different species do not exhibit phase synchronization. Even different populations of the same species do not always exhibit a peak density at the same time of the year. Furthermore even the same population displays a phase instability during successive years of study. For instance *Xerolenta obvia* from Paleokastro peaked either in January or in April (φ_j in Table I). *X. obvia* from Karvali peaked in July. *Helix lucorum* displayed a similar interannual instability. In both cases the shift in phase seems to be associated with an unexpected change of the weather, an extended dryness (STAIKOU *ET AL.*, 1988: fig. 2) which provoked an overall decline of the population density (Fig. 2).

The phase expressed as months after minimum population densities (φ_m) (Table I) is a measure of the rate of population increase from absolute minimum to peak densities. φ_m might have lower values when the time needed for a species to mature is short. Minimum φ_m values were estimated for *X. obvia* in Paleokastro, the 1st and the third year of study, indicating a rapid population growth which occurs in a period of about 3 months (Fig. 2). In Karvali, where *X. obvia* gets mature in 2 years, φ_m value was larger (Table I), as was the case with *M. cartusiana* in 1985. *Helicella (Xerothracia) pappi* snails that need 2-3 years to mature exhibited larger φ_m values, and *H. lucorum* snails which need 3-4 years exhibited the largest value of all except in 1983.

Species that mature in one year, exhibit a very rapid population growth just after the adverse period, which is winter, and consequently they are positively skewed. Species that mature in 2-3 years are negatively skewed (Table II, Fig. 3). In this case the phenological pattern may be positively skewed or symmetrical but the population remains active for longer periods and the phenological pattern is platycurtic (Table II, Fig. 3). Whereas species that mature in one year usually display a leptocurtic phenology (Table II, Fig. 3). The only species population that showed both a negatively and a positively skewed phenological pattern was *H. lucorum*.

The positively skewed phenograms are leptocurtic when they concern snail species populations that mature in one year whereas they may be slightly platycurtic when they live in regions where favourable conditions last longer as is the case of *Xeropicta arenosa* Ziegler in Edessa. Pluriennial snail species popula-

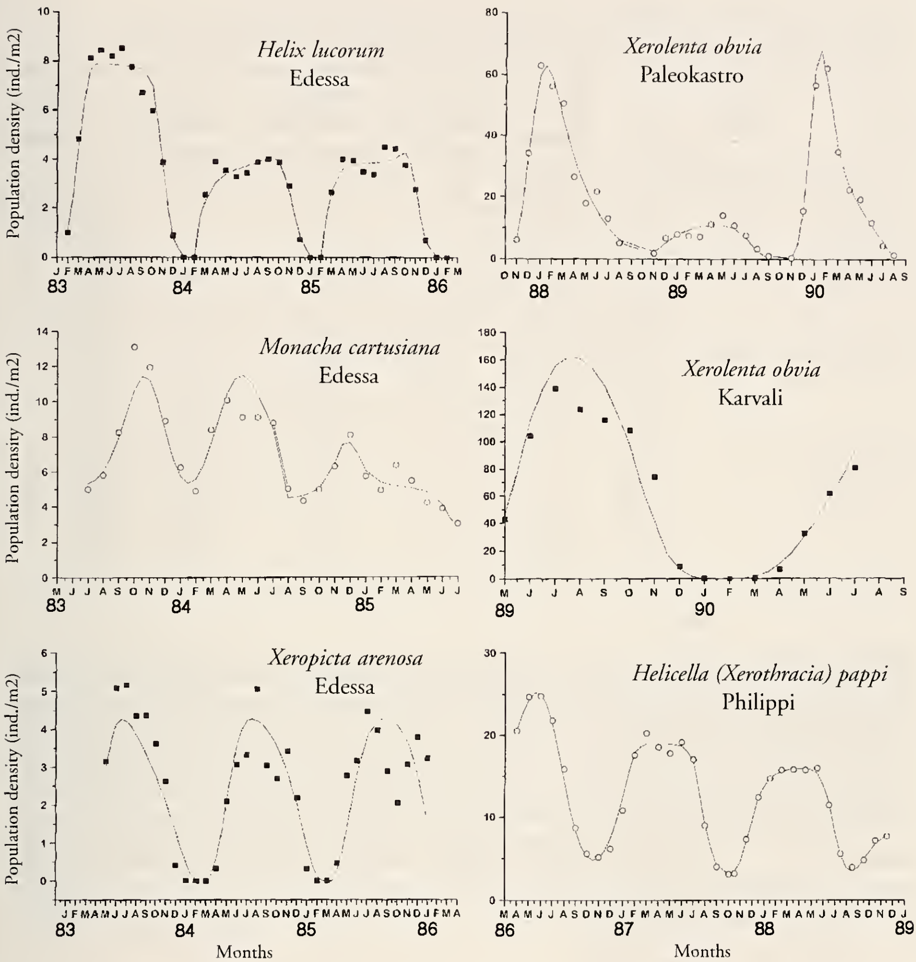

Figure 2. Abundance variations of Helicoidea snails from Northern Greece. Line: model estimates; asterisks: observations.

Figura 2. Variaciones de la abundancia de caracoles helícidos del Norte de Grecia. Línea: estimaciones del modelo; asteriscos: observaciones.

tions usually exhibit platycurtic phenological patterns, too, since their adults diapause and hide in the soil or under plants and do not emerge massively. Negatively skewed and symmetric phenograms are usually platycurtic.

It seems that there are no negatively skewed-leptocurtic species except for *M. cartusiana* that is negatively skewed and slightly leptocurtic.

Maximum activity duration is about the same for different populations of the same species or for the same population during successive years of study (Table I, MA column).

In Northern Greece long-lived species are of big size and short-lived are of small size (χ^2= 9.983, P= 0.001). Additionally, short-lived species breed in autumn whereas long-lived species may breed in autumn or vernal-estival period (χ^2= 4.261, P= 0.039) (Table III). In Northern Greece bigger helicids may breed during the vernal-estival or

Table I. The estimated parameters of the fitted model in standard time units (months).
Tabla I. Parámetros estimados del modelo ajustado en unidades de tiempo standard (meses).

Species	Place	Year	Period T (Months)	Phase φj (Months after January)	Phase φm (Months after minimum density)	Maximum activity period MA (Monthts)	R^2	Years up to matutity
Helicella pappi	Philippi	1987	12.6	2.9	5.9	7.1	0.93	2-3
		1988	10.5	3.4	6.8	6.9	0.95	
Xerolenta obvia	Karvali	1990	12.6	6.7	4.7	4.4	0.79	2
	Paleokastro	1988	14.2	0.3	2.9	4.2	0.84	1
		1989	10.8	3.5	5.7	7.3	0.77	
		1990	10.4	0.2	2.8	2.9	0.91	
Xeropicta arenosa	Potidea	1979	12.7	6.1	5.5	5.1	0.87	1
		1980	11.2	6.2	3.1	6.9	0.88	
	Edessa	1984	12.5	6.6	4.9	6.7	0.69	1
		1985	12.3	7.8	5.8	6.9	0.68	
Monacha cartusiana	Edessa	1984	6.5	-2.4	3.7	3.2	0.53	1
		1985	13.0	-1.1	6.2	4.3	0.45	2
Helix lucorum		1983	12.5	4.1	5.0	8.1	0.94	3-4
		1984	12.0	8.4	7.9	8.5	0.84	
		1985	12.0	8.9	8.5	8.2	0.86	

Table II. Skewness (negatively skewed <0.5; positively skewed >0.5) and curtosis (leptocurtic <0.5; platycurtic >0.5) from the phenograms of Helicoidea snails from Northern Greece). Abbreviations: Phil: Philippi; Pal: Paleokastro area; Kar: Karvali; Pot: Potidea; E: Edessa (the paranthesis means slightly).
Tabla II. Desviación (desviado negativamente <0,5; desviado positivamente >0,5) y curtosis (leptocúrtico <0,5; platicúrico >0,5) en los fenogramas de caracoles helícidos del Norte de Grecia. Abreviaturas: Phil: Philippi; Pal: Paleokastro area; Kar: Karvali; Pot: Potidea; E: Edessa (los paréntesis significan ligeramente).

Species	Place and Year	Positively skewed	Negatively skewed	Symmetric	Leptocurtic	Platycurtic	Mesocurtic	Years up to maturity
Helicella pappi	Phil. 1987			(+)		+		2-3
	1988		+			+		
Xerolenta obvia	Paleo. 1988	+			+			1
	1989			(+)		+		
	1990	+			+			
	Karv. 1990	+			+		(+)	2
Xeropicta arenosa	Potid. 1979				+		(+)	1
	1980	+				+		
	Edes. 1984	+				+		1
	1985	+				+		
Monacha cartusiana	Edes. 1983		+		(+)			2
	1984			+			+	1
	1985	+		(+)	+			2
Helix lucorum	Edes. 1983	+				+		3-4
	1984		+			+		
	1985		+			+		

autumnal period and small ones breed mainly in autumn (χ^2= 4.261, P= 0.039) (Table III). In coastal areas the duration of the reproductive period is very short whereas in the inland areas it is variable according to the species.

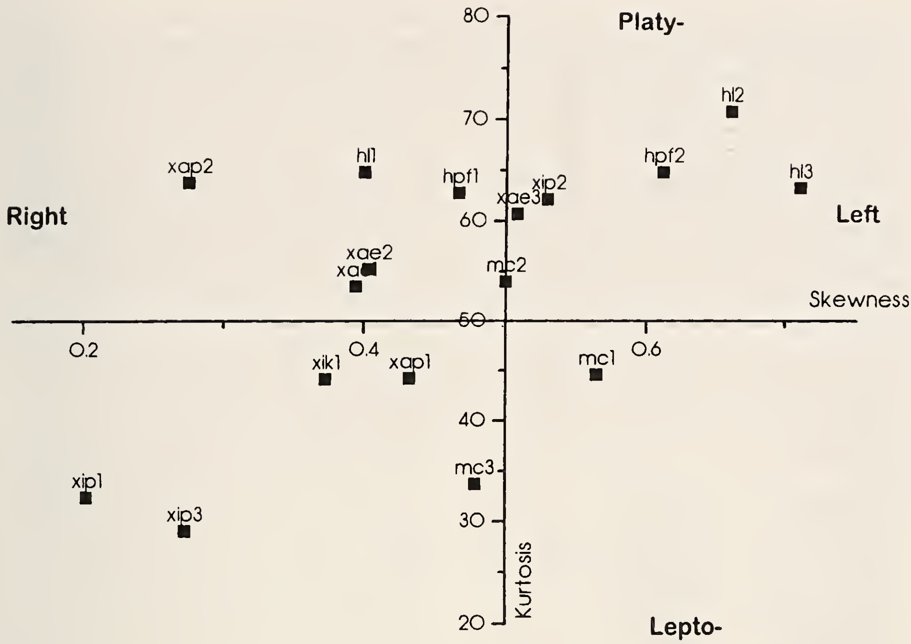

Figure 3. Ordination of phenograms into skewness(S)- curtosis (C) plane (Skewness: negatively skewed< 0.5; positively skewed> 0.5. Curtosis: leptocurtic< 0.5; platycurtic> 0.5) of Helicoidea snails from Northern Greece. Numbers denote 1st, 2d or 3d generation. Abbreviations, xap: *Xeropicta arenosa* Potidea; xae: *Xeropicta arenosa* Edessa; hl: *Helix lucorum*; hpf: *Helicella pappi* Philippi; mc: *Monacha cartusiana*; xip: *Xerolenta obvia* Paleokastro.

Figura 3. Ordenación de fenogramas respecto al plano desviación (S)- curtosis (C) (Desviación: negativa< 0,5; positiva> 0,5. Curtosis: leptocúrtico< 0,5; platicúrtico> 0,5) de babosas de la familia Helicoidea del Norte de Grecia. Los número denotan las primera, segunda y tercera generaciones. Abreviaturas, xap: Xeropicta arenosa *Potidea; xae:* Xeropicta arenosa *Edessa; hl:* Helix lucorum*; hpf:* Helicella pappi *Philippi; mc:* Monacha cartusiana*; xip:* Xerolenta obvia *Paleokastro.*

DISCUSSION

In Northern Greece the climatic conditions are not uniform (HATZIIOANNOU ET AL., 1989). The ombrothermic diagram for Northern Greece (Fig. 1) from 1980 to 1990 shows that the dry season is from June to October, whilst the wet season is divided by a cold winter period. Breeding may take place almost in all seasons except during winter. In Northern Greece, snails mainly breed from April to the end of autumn. The strong seasonality of the climate imposes a seasonal pattern of breeding. Consequently, there are two main breeding periods: the autumnal breeding period starts with the first rainfalls and stops with low temperatures (LAZARIDOU-DIMITRIADOU, 1981; STAIKOU AND LAZARIDOU-DIMITRIADOU, 1991) and the vernal-estival breeding period which starts when the mean monthly temperature rises over 10°C and stops when the arid period starts (LAZARIDOU-DIMITRIADOU, 1981; LAZARIDOU-DIMITRIADOU AND KATTOULAS, 1985; STAIKOU ET AL., 1988). Most of the land snails though, mainly short-lived and small snails, breed during the autumnal period (Table III) as Helicoidea species from Southern Europe do (CHATFIELD, 1968; REAL AND REAL-TESTUD, 1983; HELLER, 1982; SACCHI,

Table III. Life cycle characteristics from Helicoidea snails from Northern Greece. Abbreviations: D: largest shell diameter. Ehinos is found in Rhodope area, Edessa and Thessaloniki in North Central Macedonia, Philippi and Karvali near Kavala, and Paleokastro and Potidea in Chalkidiki. Abbreviations, Y: years up to maturity; SL: short lived < 3 years; LL: long lived > 3 years; SS: small sized D < 25 mm; LS: large sized D > 25 mm; V: vernal-estival reproductive period; A: automnal reproductive period.

Tabla III. Características del ciclo de vida de los caracoles helícidos del Norte de Grecia. Abreviaturas: D: mayor diámetro de la concha. Ehinos se encuentra en el área de Rhodope, Edessa y Thessaloniki al Norte de Macedonia, Phillipi y Karvali cerca de Kavala, y Paleokastro y Potidea en Chalkidiki. Abreviaturas, Y: años hasta la madurez; SL: vida corta < 3 años; LL: vida larga > 3 años; SS: pequeña talla D < 25 mm; LS: gran talla D > 25 mm; V: periodo reproductivo estival; A: periodo reproductivo otoñal.

Species	Locality	Longitude	Latitude	Y	SL	LL	SS	LS	V	A
Helix pomatia rhodopensis	Ehinos	24° 58′ 34″	41° 16′ 50″	3		+		+	+	
Helix lucorum	Edessa	22° 3′ 14′	40° 47′ 47″	3-4		+		+	+	
Monacha cartusiana				2	+		+			+
(rarely)				1	+		+		+	
Bradybaena fruticum	Edessa			2		+	+		+	
Cepaea vindobonensis	Edessa			2		+		+	+	
Helix figulina	Thessaloniki	22° 57′ 29″	41° 24′ 26″	2		+		+		+
Theba pisana	Thessaloniki			2	+		+			+
Xerotricha conspurcata	Thessaloniki			1	+		+			+
Eobania vermiculata	Thessaloniki			2		+		+		+
Helicella (Xerothracia) pappi	Philippi	24° 15′ 48″	41° 2′ 26′	2-3	+		+			+
Xerolenta obvia	Paleokastro	23° 25′ 9″	40° 24′ 59″	1	+		+			+
	Karvali	24° 30′ 11″	40° 59′ 44″	2	+		+			+
Xeropicta arenosa	Potidea	23° 19′ 24″	40° 11′ 24″	1	+		+			+
	Edessa	22° 3′ 14″	40° 47′ 47″	1	+		+			+
Cernuella virgata	Potidea	23° 19′ 24″	40° 11′ 24″	1	+		+			+

1971; BONAVITA AND BONAVITA, 1962; DEBLOCK AND HOESTLANDT, 1967) and only some breed during the vernal period as land snails from Northern Europe do (POLARD, 1975; WOLDA AND KREULEN, 1973). *M. cartusiana*, which is of Northern origin, breeds in both seasons (STAIKOU AND LAZARIDOU-DIMITRIADOU, 1990). Estival breeding period happens in places with a wet climate during summer months (STAIKOU *ET AL.*, 1988). In areas where different species coexist (as in Logos area in Edessa) although the climatic conditions are the same the species do not breed during the same period provoking less antagonistic intraspecific reactions to their hatchings (STAIKOU *ET AL.*, 1988). Semelparous species with an r-strategy synchronize their breeding period with the favourable period which is October-mid November (LAZARIDOU-DIMITRIADOU, 1981, 1995; LAZARIDOU-DIMITRIADOU AND KATTOULAS, 1985).

There is also a marked difference between the snail species living along the sea shore and the inland ones. Coupling and laying of eggs is more or less synchronous for the populations living along the seashore and do not last more than a week each. On the contrary breeding lasts about a month for the inland species (LAZARIDOU-DIMITRIADOU, 1981; STAIKOU AND LAZARIDOU-DIMITRIADOU, 1991).

The climatic conditions under which the land molluscs live do not only affect the time of the breeding season but also their whole life cycle and phenologies. *X. obvia* needs two years to mature in coastal or semi-coastal areas and one year on the mountains (e. g. Paleokastro, Central Chalkidiki, unpublished data). Similarly, *M. cartusiana* which is of northern origin needs two years to mature in the south instead of one, because it has to face the summer aestivation, although 15% of its population in Edessa tends to be semelparous (STAIKOU AND LAZARIDOU-DIMITRIADOU, 1990), as in Northern Europe (CHATFIELD, 1968).

Species like *B. fruticum* and *E. vermiculata* which are iteroparous and univoltine species, living for a few years, exhibit no seasonal trend of abundance but fluctuate almost randomly during the year. These show rather stable patterns despite the oscillations of environmental parameters. All the rest of the studied Helicoidea species can encounter seasonality by adjusting the timing of their vital activities. They respond to the adverse period of the year, which is winter time for Northern Greece, by displaying asymmetric (positively or negatively skewed phenograms) seasonal patterns of abundance variation. These patterns reflect a differential response of the species to tolerance against stress which seems not to be region-specific but species-specific. The annual or biennial r-strategists (*X. arenosa*, *X. obvia*) show a positively skewed phenological pattern due to the rapid development of juveniles soon after the adverse winter period. These juveniles have been hatched in autumn but stayed buried in the soil during winter. Their growth stops before summer dryness during which the genitalia and the gonad maturation take place and the snails are ready to lay eggs before their death in autumn. On the contrary, populations of pluriennial species are characterized by low abundance during the onset of the adverse period and a negatively skewed or symmetric phenological pattern. It seems that the growth rate of juveniles is much slower than that of annual species. The only species population that showed both a negatively and a positively skewed phenological pattern was *H. lucorum*. However, a positively skewed pattern in 1983, that is a rapid growth of population density was probable just after the adverse period since a massive emergence from hibernation of adult snails took place because of good weather conditions which started earlier than usually (STAIKOU *ET AL.*, 1988: fig. 2). Additionally, this species has a low net reproductive rate (Ro = 0.9) and a low annual turnover ratio (P/B = 1.24), the snails live up to 12 years and they mature after the third year of their lives (STAIKOU *ET AL.*, 1988).

Negatively skewed and leptocurtic phenograms could not be characteristic of a snail species since it would mean that this population would grow slowly and steadily during the favourable period of the year and would introduce rapidly growing immature snails just before the adverse period. This would be possible only if immature snails were more resistant and tolerant to the stress. Such a phenology has not also been recorded in acari or collembola (STAMOU *ET AL.*, 1993; SGARDELIS, SARKAR, ASIKIDIS, CANCELA DA FONCECA AND STAMOU, 1993). However, *M. cartusiana* is a case of negatively skewed and slightly leptocurtic phenology. In this population 15% of juveniles mature in one year as it happens in Northern Europe. So, in 1984 the dry season (summer time) was interrupted by a wet period (STAIKOU *ET AL.*, 1988: fig. 2) and this 15% of juveniles, which had already matured, managed to lay eggs before the majority of the snails which were mature and ready to copulate and lay eggs in autumn. This population, though, comes from Northern Europe and it is found in the southern limits of its distribution.

To sum up, environmental variables in Northern Greece are strongly seasonal and thus Helicoidea snails exhibit predictable oscillations in their activity patterns, which can be interpreted by the demographic response of the populations as it has been found with soil microarthropods (STAMOU *ET AL.*, 1993; SGARDELIS *ET AL.*, 1993). The semelparous and short-lived snail species populations show a more stable phenological pattern than the biennial and pluriennial ones, who mature after the first year of their life, and they are more plastic trying to face the climatic differences from one year to the other.

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